

Benthic Infauna Recovery Following Channel Dredging in the Vicinity of Bogue Inlet, North Carolina.

Adrienne Carter, Marine Scientist; Erin Hague, Sr. Marine Scientist;
and Lauren Floyd, Marine Biologist
Coastal Planning & Engineering, Inc., Marine Science & Biological Research
2481 NW Boca Raton Blvd., Boca Raton, FL 33431

ABSTRACT

Infauna are good bioindicators of natural and anthropogenic disturbance. In this study we examine responses of infauna to channel modification at Bogue Inlet, NC. Sampling data was assessed using a Before-After-Control-Impact (BACI) design for identifying the infaunal population dynamics following dredging activities. Sites were core sampled for three years to determine macroinvertebrate community structure at three habitat types within the inlet complex. Four baseline monitoring events provided pre-construction macroinvertebrate community structure data. Inlet channel realignment occurred in 2005, followed by seasonal monitoring at each site throughout 2006 and 2007. By use of multivariate analysis, the effects of inlet relocation on the macroinvertebrate community were assessed at the habitat level, as well as temporal and spatial variation occurring within the communities. Patterns of succession were also evaluated. Overall results show the number of species and the abundance of organisms within species as significantly higher post-construction, with the exception of the intertidal habitat. Community changes overall appeared to be driven by the introduction of, or replacement of, a single species within a habitat. An overall increase in polychaete and bivalve species abundance post-construction indicates that the initial project disturbance, found at the main ebb habitat, has abated and that Stage I of the pattern of succession is present. Fluctuations in community composition identified at the intertidal and marsh habitats may be due to inherent ecosystem processes.

1.0 INTRODUCTION

In North Carolina the usefulness of macroinvertebrate monitoring as a tool for impact assessment continues to be debated amongst researchers and leading regulatory agencies. For this particular project, the State and Federal agencies required four years of monitoring in three different habitat types. The monitoring plan was developed in support of an Environmental Impact Statement for the Bogue Inlet Channel Relocation Project. The monitoring plan was intended to assess and document the potential effects of project activities on infaunal species at three habitat types and a control found within the inlet system.

Sample sites were determined by areas of potential direct and indirect impacts, where biological and physical conditions were most likely to be affected by project related activities. All three habitat types and the control were core sampled for three years to determine macroinvertebrate community structure in the vicinity of Bogue Inlet. Four baseline monitoring events provided pre-construction macroinvertebrate community

structure per habitat type, including spatial and temporal variations. Inlet channel realignment occurred in March and April 2005, followed by seasonal monitoring at each site throughout 2006 and 2007.

Multivariate analyses were performed to determine project related effects at the habitat level, as well as temporal and spatial variation occurring within these habitats. Recovery of macroinvertebrate assemblages to a disturbance has been shown to follow a predictive sequence of community changes. Generally, amphipods exhibit quick population responses to disturbance events due to their direct development (i.e., fertilization is internal). Numerous small tube-dwelling polychaete species and small bivalves are opportunistic pioneering species that colonize surficial sediments once a disturbance has abated.

2.0 METHODOLOGY

2.1 Site Selection

Macroinvertebrate/infaunal monitoring sites were established in 2003 and 2004. The sites were chosen to reflect a representative sample of infaunal and macroinvertebrate habitats near the areas of direct and indirect impacts. These sample sites include three intertidal sites (Sites 1 through 3), three main ebb channel sites (Sites 4 through 6), a main ebb control site (Site 7), and three backbarrier marsh sites (Sites 8 through 10) (Figure 1). Marsh Site 8 was relocated in October 2004 to the southeast side of Dudley Island after completion of the pre-construction sampling events to monitor possible sedimentation effects near the south side of Dudley Island. As the original location of Site 8 was changed no baseline data was available; therefore this data was not included in the marsh data analyzed in this report.

Due to the natural migratory nature of Bogue Inlet, the horizontal positioning of the sampling stations shifts in response to the fluctuating conditions within the inlet complex. However, all attempts were made to keep the vertical location of each sample the same (between +2.29 and -1.59 NGVD) at each site. When CZR, Inc. biologists conducted the initial pre-construction sampling events, the location of Sites 1 and 2 were offset due to the fact that the initial coordinates utilized were estimated from aerial photography. Therefore, an adjustment in the location of Sites 1 and 2 was necessary to ensure that sampling at these sites remained representative of the intertidal environment adjacent to the pre-construction channel location. Additionally, shoreline erosion occurring north of the Coast Guard Channel on Bogue Banks influenced the subsequent relocation of Sites 1 and 2 (Figure 1). Considering these two factors, by the end of the 2007 sampling events Site 1 was relocated, on average, 406 feet from the pre-construction April 2003 location. Site 2 was relocated an average of 397 feet from the pre-construction April 2003 location. These averages were calculated by comparing Global Positioning System (GPS) coordinates collected during field operations. Site 3 was relocated, on average, 124 feet from the April 2003 location post-construction due to the migration of the sand spit from the ocean front shoreline to the inlet shoreline. Sites 4, 5, and 6 were repositioned as needed to avoid potential safety hazards during sampling efforts as these sites are located in the high energy environment of the main ebb channel.

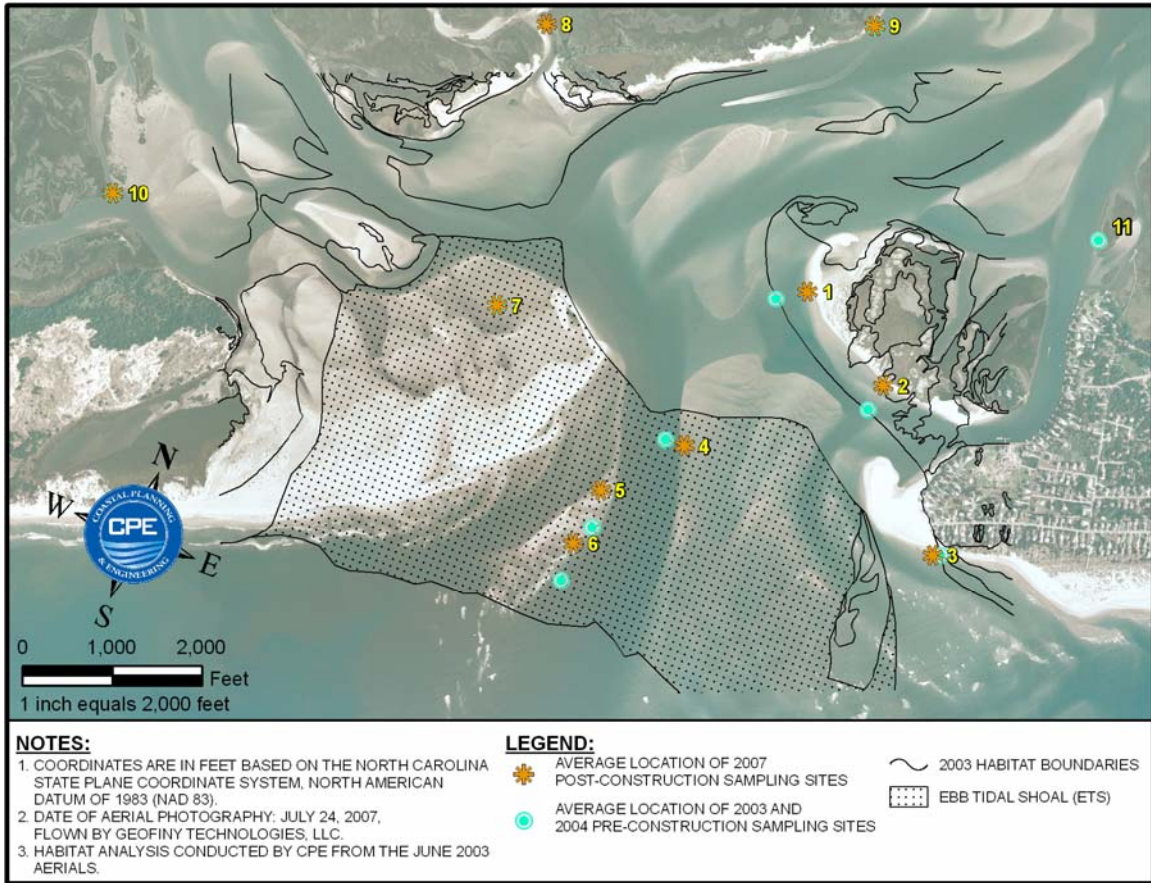


Figure 1. Pre-construction and post-construction mean sampling sites located in the Bogue Inlet complex, North Carolina. The habitat boundaries illustrate the 2003 channel alignment and the ebb tidal shoal boundary pre-construction.

2.2 Sampling Efforts

Baseline (pre-construction) monitoring occurred during April, July, and October 2003, with the final baseline monitoring event occurring in January 2004. Once construction was completed in April 2005, CZR, Inc. biologists resumed seasonal macroinvertebrate/ifaunal sampling in January, April, July and October 2006 to characterize species common to each habitat type. The second year of post-construction monitoring repeated seasonal sampling events in January, April, July and October 2007.

Quantitative sampling of infaunal organisms occurred at low tide. During each pre- and post-construction sampling event, CZR, Inc. biologists used a handheld PVC coring device, 10 cm in diameter and 15 cm long, to collect samples at the established sampling sites. Three replicate samples per site (30 samples total) were collected to a depth of 15 cm and sieved through a 541 μm mesh sieve bucket. Each sample was transferred into labeled vials and fixed with a 10% formalin solution to preserve the organisms, and then all samples were transported to the laboratory for analysis. Samples were sorted and organisms were identified to the lowest taxonomic level. After identification analysis, representative samples were transferred to a 50 percent isopropynol preservative for long term storage.

2.2 Data Analysis

Total number of individuals from each taxa (usually species, but occasionally genus or family), the number of species (S), total number of organisms (N), Shannon Diversity Index (H'), Simpson's Index (1-D), Margalef's Index (d), and Pielou's Index of Evenness (J') were calculated for each site per construction and for each habitat type per construction.

Multivariate analysis were performed using PRIMER software package (Plymouth Routines In Multivariate Ecological Research, Plymouth Marine Laboratory, UK), Bray-Curtis similarity coefficients were determined from the species site matrix after log (X+1) transformation, and a multi-dimensional scaling plot (MDS) constructed to represent similarities of infaunal communities at each sampling event and at each habitat type (Clark and Warwick, 1994). Analysis of similarity (ANOSIM) was performed to examine the significant differences between communities at each habitat type pre-construction and post-construction. Diversity indices were performed on non-transformed data.

3.0 RESULTS

The sampled infaunal community at the nine sites located in the vicinity of Bogue Inlet during the pre- and post-construction events was primarily composed of a variety of worms, crustaceans, and bivalves. The Class composition of the dominant fauna recorded, and pooled for at all nine sites during all pre, one year post-, and two year post-construction sampling events is shown in Figure 2.

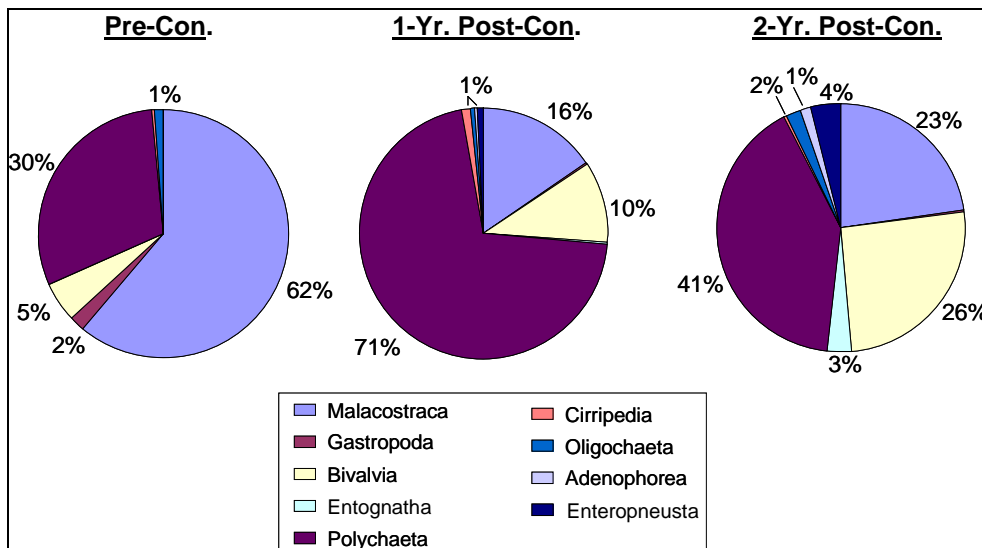


Figure 2. Class composition of the dominant fauna recorded, and pooled for at all sites during the pre-construction, 1-year post-construction, and 2-year post-construction sampling events

3.1 Faunal density

Faunal density is the number of individuals found per habitat type. A total of 36 taxa (N=548) were recorded during the 2003-2004 pre-construction sampling events. During the 1-year post-construction 2006 sampling events, a total of 51 taxa (N=1608) were recorded. The total number of taxa recorded during the 2007 2-year post-construction sampling events was 70 (N=1182).

3.2 Faunal Composition at each Habitat Type

Intertidal (Sites 1 to 3): Figures 3a-3f illustrate the intertidal species and Class composition present during the 12 sampling events (4 pre-construction, 4 1-year post-construction and 4 2-year post-construction). A total of 9 species were present during pre-construction with *Emerita talpoida* (53%), *Scolelepis squamata* (23%) and *Neohaustorius schmitzi* (11%) being most abundant (4 species with <1% contribution were combined into “other” in Figure 3a). Malacostraca was the dominant Class (72%) during pre-construction (Figure 3b). Seventeen species were recorded during 1-year post-construction sampling (8 species with <1% contribution were combined into “other” in Figure 3c). *Donax variabilis* abundance increased from 5% to 11%. *Scolelepis squamata* decreased from 23% to 11%, while *Emerita talpoida* decreased from 53% to a relative of abundance of 43% one year post-construction. While Malacostraca was still the dominant Class, it decreased in abundance to 59%, accompanied by an increase in relative abundance of polychaetes and bivalves (Figure 3d). The total number of species increased to nineteen two years post-construction (9 species with <1% contribution were combined into “other” in Figure 3e). From 1-year to 2-year post-construction, *Emerita talpoida* decreased to <1%, while *Scolelepis squamata*, *Donax variabilis* and *Neohaustorius schmitzi* increased in relative abundance by 3%, 9% and 24% respectively. Class Malacostraca continued to decrease, and chaetognaths (Class Sagittoidea) appeared and accounted for 14% of the infauna documented 2-years post-construction (Figure 3f).

Main Ebb (Sites 4 to 6): Species and Class composition for pre-construction, 1-year post-construction and 2-year post construction in the main ebb sites are shown in Figures 4a-4f. A total of 17 species were recorded during pre-construction with *Acanthohaustorius* sp. (19%), *Leitoscoloplos fragilis* (15%), *Bathyporeia parkeri* (12%), *Paraonis fulgens* (10%) the most dominant species recorded (5 species are included in “other” in Figure 4a). Malacostraca was the dominant Class during pre-construction (Figure 4b). Eighteen species were documented during the 1-year post-construction events (13 species are included as “other” in Figure 4c). The bristle worm *Scolelepis squamata* increased considerably from 9% pre-construction to a relative abundance of 78% one year post-construction. One year post-construction relative abundance of *Donax variabilis* and *Emerita talpoida* increased by 1% each. Polychaetes increased from 36% pre-construction to 86% 1-year post-construction, replacing Malacostraca as the dominant Class during these monitoring events (Figure 4d). Two years post-construction there were 22 species documented at the main ebb sites (15 species are included as “other” in Figure 4e). Notably, the coquina clam *Donax variabilis* became the most abundant (63%) species recorded during the 2007 post-construction sampling events, with a 56% increase from the previous year. The increase in abundance of *Donax*

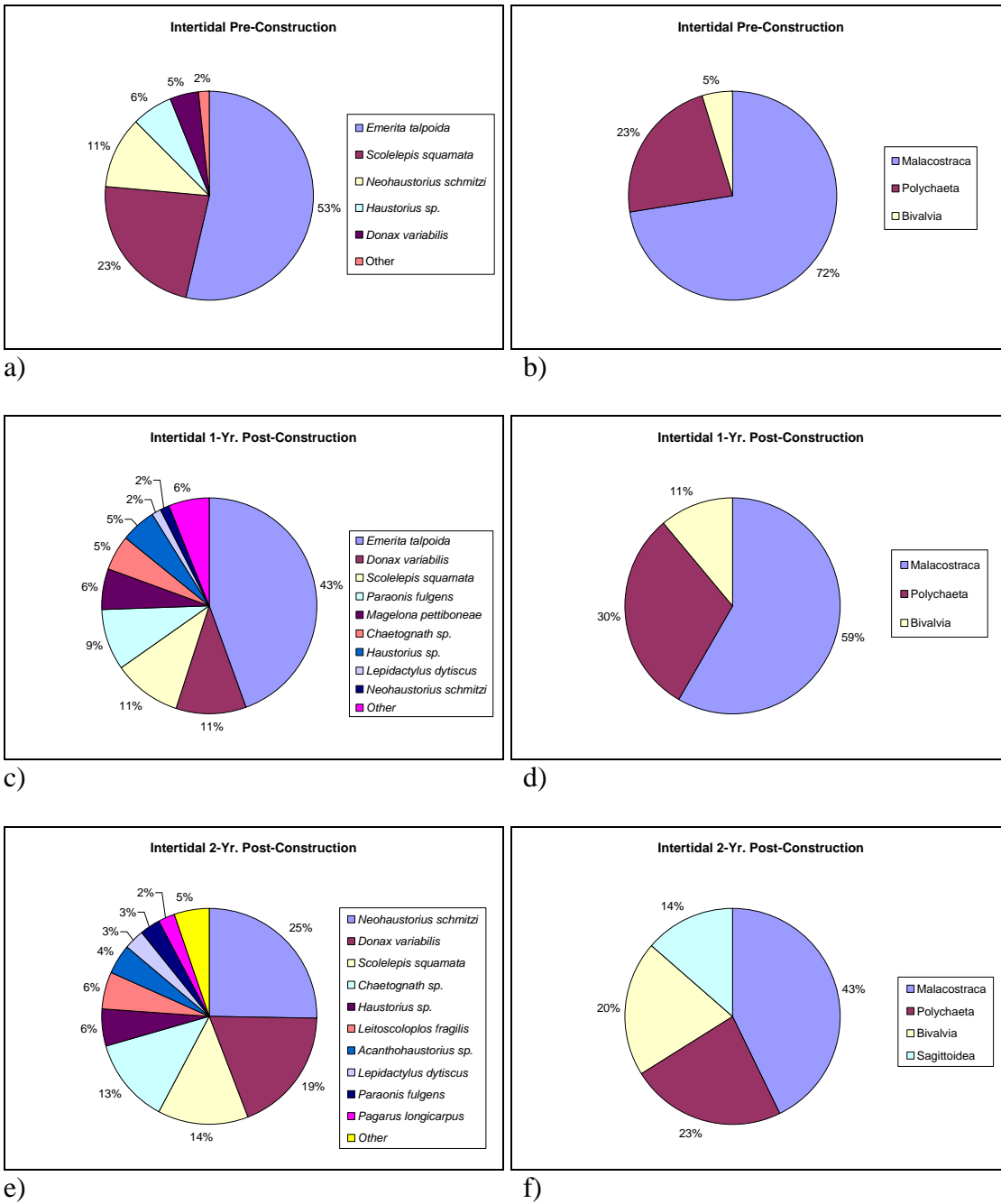
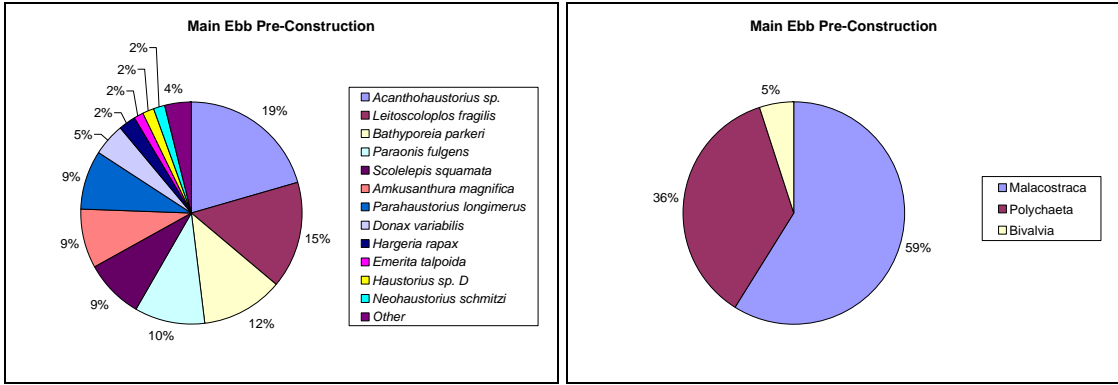
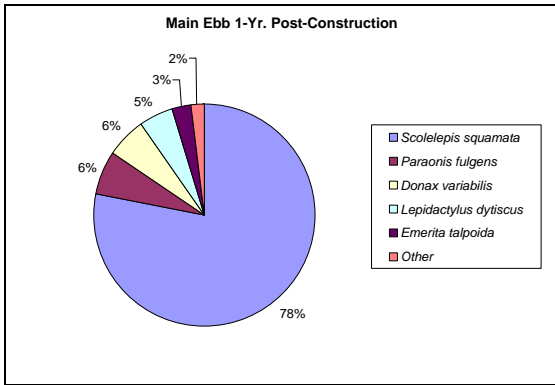


Figure 3. Intertidal Island (Sites 1 to 3) a) pre-construction species composition; b) pre-construction Class composition; c) 1-yr. post-construction species composition; d) 1-yr. post-construction Class composition; e) 2-yr. post-construction species composition; f) 2-yr. post-construction Class composition.

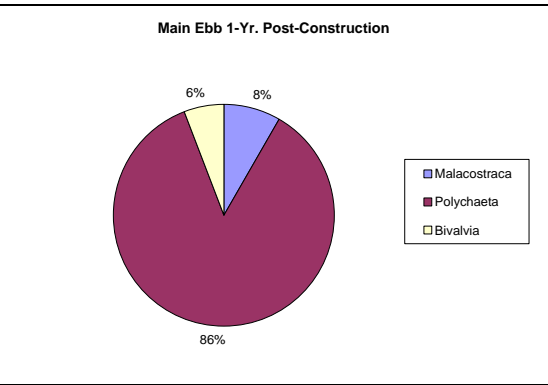


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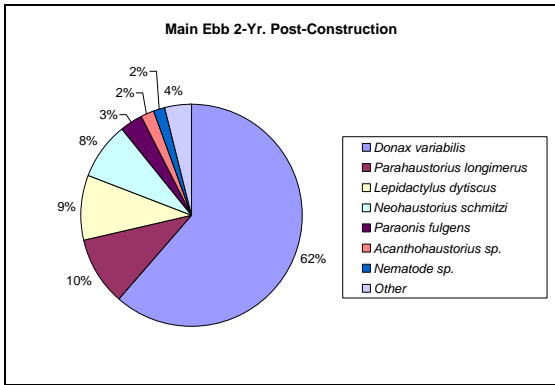
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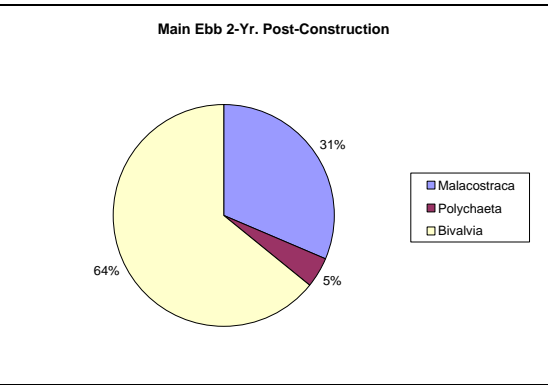
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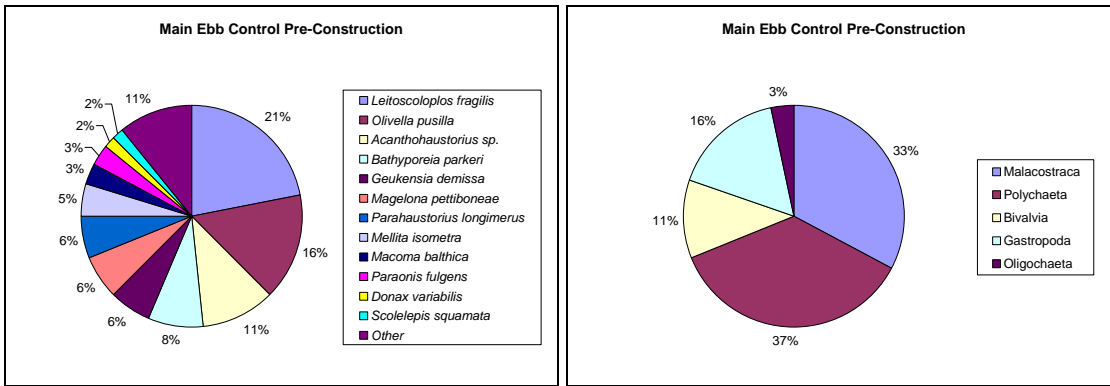


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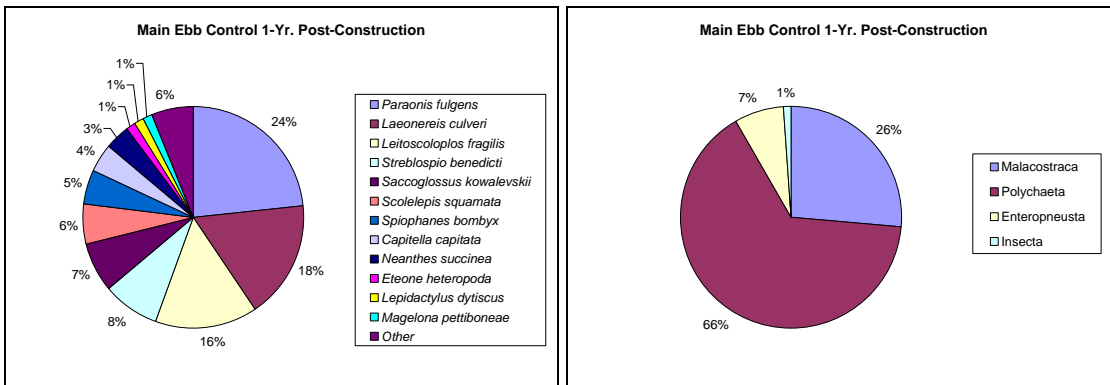
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Figure 4. Main Ebb (Sites 4 to 6) a) pre-construction species composition; b) pre-construction Class composition; c) 1-yr. post-construction species composition; d) 1-yr. post-construction Class composition; e) 2-yr. post-construction species composition; f) 2-yr. post-construction Class composition.



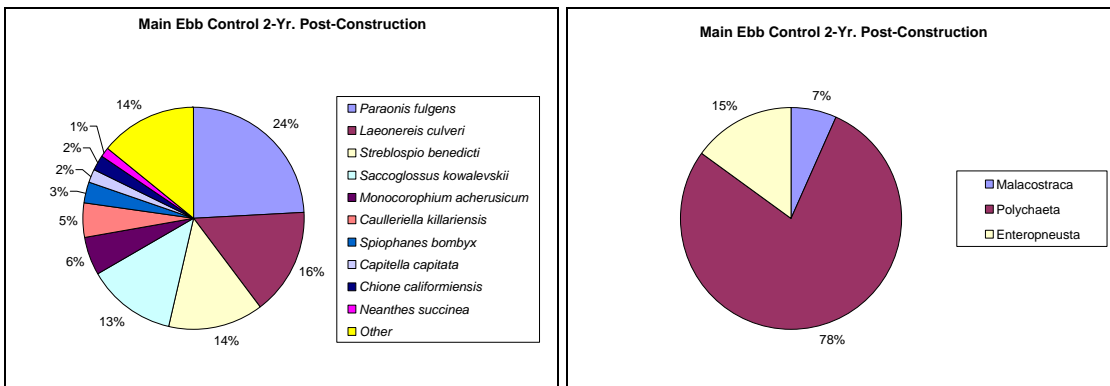
a)

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Figure 5. Main Ebb Control (Site 7) a) pre-construction species composition; b) pre-construction Class composition; c) 1-yr. post-construction species composition; d) 1-yr. post-construction Class composition; e) 2-yr. post-construction species composition; f) 2-yr. post-construction Class composition.

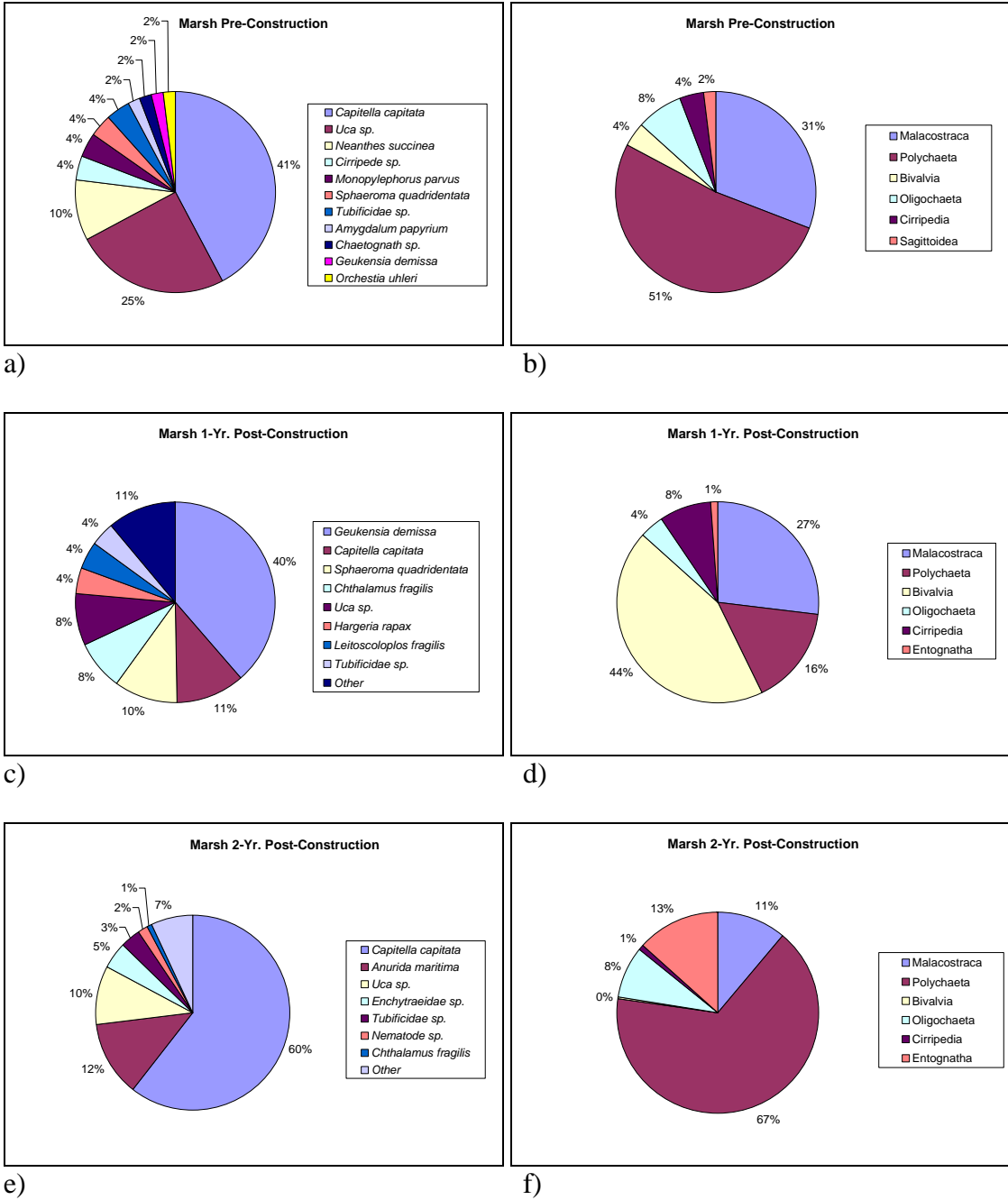


Figure 6. Marsh (Sites 9 and 10) a) pre-construction species composition; b) pre-construction Class composition; c) 1-yr. post-construction species composition; d) 1-yr. post-construction Class composition; e) 2-yr. post-construction species composition; f) 2-yr. post-construction Class composition.

variabilis led to Bivalvia becoming the dominant Class two years post-construction (Figure 4f).

Main Ebb Control (Site 7): Figures 5a-5f show the species and Class composition documented at the control site for the main ebb habitat type for the three years of infauna sampling. Twenty species were recorded at this site pre-construction, with *Leitoscoloplos fragilis* the dominant species found (21%) (8 species are included as “other” in Figure 5a). Polychaeta and Malacostraca dominated the control site during pre-construction, with 37% and 33% abundance, respectively (Figure 5b). Twenty-one species were found one year post-construction, with *Paraonis fulgens* the most abundant species (24%) (9 species included as “other” in Figure 5c). The deposit feeding polychaete *Laeonereis culveri* were documented with 18% abundance one year post-construction. Polychaetes dominated this site in 1-year post construction monitoring (Figure 5d). The total number of species increased to 34 two years post-construction, with *P. fulgens* still the most abundant at 24% and *L. culveri* was still present at 16% (24 species with <1% abundance are included as “other” in Figure 5e). Polychaeta remained the dominant Class, with 78% abundance (Figure 5f).

Marsh (Sites 9 & 10): Figures 6a-6f show the species and Class composition recorded at the marsh habitat sites during the pre-, 1-year post-, and 2-year post-construction sampling events. Eleven species were found pre-construction, with *Capitella capitata* and *Uca* sp. the most abundant species, at 41% and 25% respectively (Figure 6a). Polychaeta was the dominant Class found in the marsh sites pre-construction (Figure 6b). The number of species found in the marsh sites increased to 20 during 1-year post-construction, with *Geukensia demissa* and *Capitella capitata* the most abundant species at 40% and 11%, respectively (12 species with <1% abundance are included as “other” in Figure 6c). The increase in abundance of the ribbed mussel *Geukensia demissa* led to Bivalvia becoming the dominant Class 1-year post-construction (Figure 6d). Twenty-three species were documented during 2-year post-construction monitoring, with *Capitella capitata* once again becoming the dominant species with 60% abundance (16 species are included as “other” in Figure 6e), accompanied by the return to Polychaeta as the dominant Class (Figure 6f).

3.3 Taxonomic Richness

Taxonomic Richness (S) is defined as the number of different taxa (i.e. species but on occasion genus) observed within a specified habitat type. Table 1 illustrates the mean number of taxa recorded per habitat type at pre-construction, 1-year post-construction, and 2-year post-construction events. As seen in Table 1, an overall increase in species richness was observed among all habitat types and the control over time.

Habitat Type	Number of Taxa (S)			Number of Organisms (N)			Shannon Diversity Index (H')			Simpson's Index (1-D)			Pielou's Index of Evenness (J')			Margalef's Index (d)		
	Pre	Post1	Post2	Pre	Post1	Post2	Pre	Post1	Post2	Pre	Post1	Post2	Pre	Post1	Post2	Pre	Post1	Post2
Intertidal (1,2,3)	9	17	19	304	151	172	1.32	2.04	2.31	0.64	0.80	0.87	0.60	0.72	0.78	1.40	3.19	3.50
Main Ebb (4,5,6)	17	18	22	127	1040	405	2.36	0.93	1.55	0.89	0.39	0.62	0.83	0.32	0.50	3.30	2.45	3.50
Main Ebb Control (7)	20	21	34	65	206	337	2.57	2.38	2.53	0.91	0.88	0.88	0.86	0.78	0.72	4.55	3.75	5.67
Marsh (9,10)	11	20	23	52	211	268	1.74	2.20	1.56	0.76	0.82	0.61	0.73	0.74	0.50	2.53	3.55	3.94

Table 1: Comparison of pre- (2003-2004), 1-year post-construction (2006) and 2-years post-construction (2007) benthic community parameters (mean values) by habitat type at Bogue Inlet, NC.

3.4 Diversity Indices

Diversity indices were calculated utilizing PRIMER at each habitat at pre-construction, 1-year post-construction, and 2-years post-construction (Table 1). Margalef's Index (d) is a measure of species diversity but with an emphasis on species richness. Simpson's Index (1-D) measures the 'evenness' of the community. Margalef's Index (d), Simpson's Index (1-D), Shannon's Index (H'), and Pielou's (J') values were all higher within the intertidal habitat both 1-year post-construction, and 2-years post-construction. Margalef's Index (d), Simpson's Index (1-D) and Pielou's (J') values were lower within the main ebb habitat 1-year post-construction, and although all values for these indices slightly increased 2-years post-construction, values were not similar to pre-construction values. Values for all indices were consistently lower 1-year post-construction at the main ebb control indicating project effects were apparent one-year post-construction. Higher values for both Margalef's Index (d) and Simpson's Index (1-D) for samples collected 1-year post-construction at the marsh habitat indicates that the abundance was more evenly distributed amongst the taxa recorded. Mean Pielou's Index values amongst the main ebb habitat was significantly lowest at 1-year post-construction indicating that the infaunal communities were not as stable (i.e., resilient) when compared to pre-construction.

3.5 Multivariate analyses

MDS analyses indicate that only two habitat types had distinct changes at the community level between pre- and post-construction (Figure 3). While the intertidal and marsh habitats remained relatively clustered for all events, the control community changed over time, as shown by the shifting of the points from the bottom of the MDS plot towards the top of the plot. The shift in the control site to the north of the plot suggests that comparable compositional changes occurred between pre-construction and post-construction. This shift suggests that the intended control site was actually impacted one year post-construction and that it continued to change two years post-construction. While the control appears to still be changing two years post-construction, the Main Ebb habitat seems to be returning to its pre-construction community, as evident by the grouping of the 2-year post-construction and pre-construction points. The northward shift of control post-construction was of greater magnitude than the shift observed for the

main ebb 1-year post-construction. This suggests that the projects effects were more severe at the control than at the main ebb habitat. Figure 3 shows that the main ebb habitat is returning to similar composition pre-construction. ANOSIM one-way analyses followed by pairwise tests of the data at the control site indicate that communities had changed significantly between pre- and post-construction ($p < 0.05$).

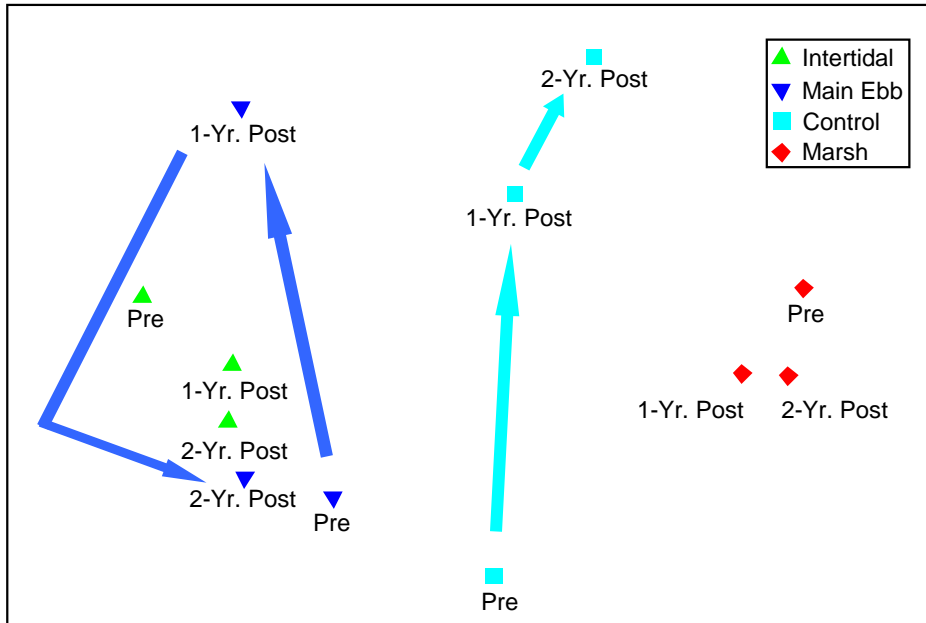


Figure 3. MDS ordination of Bray-Curtis similarities calculated after $\log(X+1)$ transformation of mean faunal abundance for each habitat type sampled during pre, 1-year post-construction and 2-years post-construction (stress = 0.1).

4.0 DISCUSSION

In comparison to the baseline results, the abundance of taxa (S) and organisms (N) were not statistically significantly higher overall post-construction with the exception of the intertidal habitats, where N decreased post-construction. Shannon diversity (H'), Simpson's Index (1-D), and Pielou's (J') values were significantly lower post-construction at the main ebb control and the main ebb habitat (Sites 4, 5, and 6). An increase in stress on a community leads to a decrease in H' , d' , and J' values (Clark and Warwick, 1994). H' , 1-D, J' , and d' values were all higher at the intertidal habitats post-construction; while J' was significantly lower at the marsh habitat post-construction. Therefore no significant change in faunal communities occurred between pre and post-construction events. The increase in dominance at the marsh habitats can be attributed to increased abundance (41%) of the ribbed mussel *Geukensia demissa* recorded during 1-year post-construction sampling events.

Considering that some species found post-construction were either rare or completely absent during the pre-construction events suggests that many of these species (which also increased in abundance post-construction) were opportunistic, colonizing species. According to Bolam and Rees (2003), early colonists generally have similar life

history patterns including short-generation times and high larval availability, which would account for the increase in abundance (N) in certain opportunistic species (e.g. *Scolecipis squamata*, *Paraonis fulgens*, and *Donax variabilis*) post-construction at the main ebb sites and the increase in polychaete species (*Paraonis fulgens*, *Laeonereis culveri*, and *Streblospio benedicti*), present year two post construction at the main ebb control. In general, research indicates that when benthic assemblages are disturbed, community diversity is reduced (Bolam and Rees, 2003; Rakocinski *et al.*, 1996; Sarda *et al.*, 2000) as was observed in the main ebb habitat and the control. However, after a disturbance the recovery of benthic assemblages has been shown to follow a predictive succession of community changes. The disturbance abates over time, and Stage I (i.e. pioneering taxa) of the benthic successional paradigm occurs. The Stage I taxa usually consist of small opportunistic polychaetes (e.g. *Paraonis fulgens*, *Laeonereis culveri*, and *Streblospio benedicti*) or bivalves and are typically represented by short-lived individuals, with the exception of *D. variabilis*. Stage I opportunistic species have the ability to colonize the surficial sediments in high numbers due to their similar life history traits (Bolam and Rees, 2003). A post-construction increase in both polychaete abundance and bivalve species is evident post-construction (Figure 2). The data shows that Stage I was initiated at the main ebb habitat and control. The pattern of succession following a disturbance is initially dominated by polychaetes; however over time, or at greater distances from an impact site, Stage II develops at which time the opportunistic taxa from Stage I are replaced by larger, longer-lived and deeper-burrowing species (Bolam and Rees, 2003; Stanos and Simon, 1980). With continued successional patterns, Stage III occurs. The late-successional (i.e., climax) Stage III assemblage consists of more diverse species, which are dominated by larger, longer-lived taxa (Bolam and Rees, 2003).

The control site (Site 7) was initially selected for having potentially representative infaunal species and hydrodynamic conditions comparable to the other main ebb sample sites. The location was chosen to reflect the infaunal species that would not be expected to receive direct or indirect effects from the project. However, the significant decrease in Shannon, Simpson's, and Pielou's Index values, and increase in species abundance at the control site, suggest that project effects occurred at the control site.

Sampling adjacent to the east and west sides of the main ebb channel (Sites 4 to 6) was initiated to provide evidence of any changes to the shoal habitat as a result of project activities. However, with the readjustment of these sites (potential spatial variation), the seasonal variation of populations, determination of how these infaunal communities reacted to project effects is quite complex (Peterson and Bishop, 2005). Benthic communities are rarely in equilibrium and can vary significantly in their distribution and biotic composition. In addition, natural ecosystem processes and physical variations make it difficult for researchers to distinguish between natural and man-induced disturbances (Grober, 1992). However the multivariate data analyses aided in determining potential project effects at the main ebb habitat. As seen in the MDS plot, these communities appear to be returning to pre-construction levels.

Macroinvertebrate body size determination was not required under the project permits. However, in order to identify recruitment class size and method (pelagic versus migration), data collection on body size is essential for future project impact studies. Recolonization of a disturbed area occurs via recruitment or migration and with the known body-size; the successional stages after a disturbance would be better identified.

5.0 CONCLUSION

An increase in stress within a community leads to a decrease in H' , d , and J' . These indices did not significantly change; therefore the intertidal habitats (Sites 1 to 3) of Bogue Inlet were not considered impacted as a result of the inlet channel modification. These sites are naturally dynamic ecosystems, experiencing regular accretion and erosion.

Index values H' , $1-D$, J' , and d , significantly decreased at the main ebb habitat (4 through 6). Combined with the significant increase in the opportunistic bristle worm *Scolelepis squamata*, effects from the inlet modification were present at this site 1-year post-construction. However due to significant decrease in abundance of *Scolelepis squamata* during the 2-year post-construction events, and the subsequent increase in H' , $1-D$, J' , and d index values, we conclude that the disturbance has abated and Stage I of the pattern of succession is present.

The control site 7 experienced project effects, and therefore cannot be considered a true control for the main ebb habitats. However, selecting a control site within a dynamic inlet proves challenging.

Donax species (Class Bivalvia) inhabit shifting sands in the turbulent intertidal zone. Levinton (1970) concluded that *Donax* are an opportunistic species that inhabit young habitats with high environmental stress. The high abundance of *Donax variabilis* at the main ebb habitat 2-years post-construction, leads to a conclusion that this environment is now dominated by physical stress, natural within high energy inlet.

Marsh habitat was dominated by the Class Polychaeta pre-construction. Bivalva were the dominant class 1-year post-construction, however this can be attributed the “clumping” nature of the ribbed mussel *Geukensia demissa*, found in high abundance 1-year post-construction. Class Polychaeta returned to similar levels at 2-year post-construction indicating that any initial project disturbance has abated.

The monitoring plan was developed with the intent of determining the rate at which the infaunal community structure recovers (e.g. total abundance, and species richness). Results from these investigations suggest that the disturbance has abated and Stage I has been achieved. Generally, amphipods (Class Malacostraca) exhibit quick population responses to disturbance events due to their direct development (i.e., fertilization is internal) (Mallin *et al.*, 1999). Numerous small tube-dwelling polychaete species and small bivalves are known as opportunistic pioneering species that colonize surficial sediments once a disturbance has abated (Bolam and Rees, 2003). Overall results show the number of species and the abundance of organisms within species as

significantly higher post-construction, with the exception of the intertidal habitat. Community changes overall appeared to be driven by the introduction of, or replacement of, a single species within a habitat. An overall increase in polychaete and bivalve species abundance post-construction indicates that the initial project disturbance, found at the main ebb habitat, has abated and that Stage I of the pattern of succession is present. Fluctuations in community composition identified at the intertidal and marsh habitats may be due to inherent ecosystem processes.

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